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A behavioral analysis of fossil bird tracks from the Haman Formation (Republic of Korea) shows a nearly modern avian ecosystem

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Abstract The Lower Cretaceous Haman Formation of the Republic of Korea has yielded several localities with thousands of dinosaur, bird, and pterosaur tracks. One such tracksite is found at the Gyeongsangnam-do Institute of Science Education (GISE) in Jinju, Republis of Korea. More than 1000 bird tracks are exposed on a single bedding plane, and thousands more are found in smaller float blocks on exhibit around the museum or in storage. The morphologic and behavioral diversity is extremely high; there are more than seven different morphologies described herein, with behaviors ranging from feeding—including pecking, probing, predator-prey interactions, and scything traces—to landing and running. Arcuate traces and associated webbed-footed trackways are identical to scything feeding traces produced by the extant black-faced spoonbill (*Palatea minor*). Individual peck and probe marks have also been reported, and clustered probing has been observed. The behaviors at this site are strikingly modern in respect to morphology and diversity, indicating that ornithurine birds had a very modern set of behaviors and anatomy. The high morphologic diversity of track morphotypes indicates that Early Cretaceous ornithurine birds were actually very diverse, compared to previous assumptions based on the body fossil record, which is dominated by enantiornithines.

Key words Aves, avian behavior, probe marks, Cretaceous bird tracks, fossil birds

1 Introduction

The study of fossil avian trackways from behavior has not been widely performed, however, there are studies that have examined the similarities between modern and fossil avian traces. Erickson et al. (1967) reported dabble marks from the Eocene Green River Formation attributed to *Presbyornis*. Lockley et al. (2009) examined the fossil tracks of *Ignotornis mcconnelli* and observed that several behaviors were similar to those produced by herons. Genise et al. (2009) examined fossil tracks from the Eocene of Argentina and compared them

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directly to traces produced by modern birds. Falk et al. (2010) described probe and peck marks from the Lower Cretaceous Haman Formation of the Republic of Korea. Our study adds to this body of work in describing traces and interpreting behavior from fossil bird tracks from an Early Cretaceous locality from the Haman Formation at the Gyeongsangnam-do Institute of Science Education (GISE) in Jinju, Republic of Korea. Herein we perform an in-depth analysis of the behavior produced at the GISE site, as well as further examination of avian tracks and traces that were not studied in detail by Kim et al. (2012).

The GISE locality is unique in that it preserves thousands of bird tracks and traces (Lockley and Harris, 2010; Kim et al., 2012). Lockley and Harris (2010) were the first to note unique arcuate traces associated with webbed-footed tracks and suggest their similarities to modern black-faced spoonbill (*Palatea minor*) tracks and traces. Kim et al. (2012) performed an in-depth mapping and ichnotaxonomic analysis of the GISE site, including a map of the paleoshoreline, and described the site as a "paradise for Mesozoic birds." Over 2500 bird tracks are distributed on two large slabs of rock between two exhibit halls. The webbed-footed bird tracks associated with the arcuate traces were assigned to a new ichnospecies of *Ignotornis* (*I. gajinensis*), and reiterated their extreme similarity in morphology and behavior to modern spoonbills.

The Haman Formation is well known for its avian tracks and traces. Kim (1969) first described bird tracks from the Haman Formation. Baek and Yang (1997, in Korean) later discussed the amount of available material. The current named ichnogenera from the Haman Formation include: *Koreanaornis hamanensis* Kim, 1969, *Ignotornis yangi* Kim et al., 2006, *I. gajinensis* Kim et al., 2012, and *Goseongornipes markjonesi* Lockley et al., 2006. *Koreanaornis* is a small, incumbent anisodactyl track that may or may not have a hallux impression. *Ignotornis yangi* is a large semipalmate track first described from the Haman Formation of Changseong and Sinsu Islands. *Goseongornipes markjonesi* is a track that is smaller than *Ignotornis* and *Hwangsangornipes* (from the Upper Cretaceous Jindong Formation; Kim et al., 2012) and is assigned to the Ignotornidae. The original description of *G. markjonesi*, however, is from two poorly preserved tracks from the Jindong Formation (Lockley et al., 2006). The GISE presents a unique opportunity to study whole-ecosystem behavioral patterns of birds, and to draw evolutionary conclusions based on trace fossil evidence.

2 Material and methods

Materials used in this study originate from the Gyeongsangnam-do Institute of Science Education (GISE) in Jinju, Republic of Korea (S.I. fig. 1). The majority of specimens are on large slabs that were found during excavation of the building's foundation. There are two separate large slabs that contain a large number of well-preserved bird and dinosaur (i.e., theropod and sauropod) tracks and trackways. The Exhibit Hall 1 site has 1500–2000 bird tracks—this does not count the isolated float blocks placed around the museum (Kim et al.,

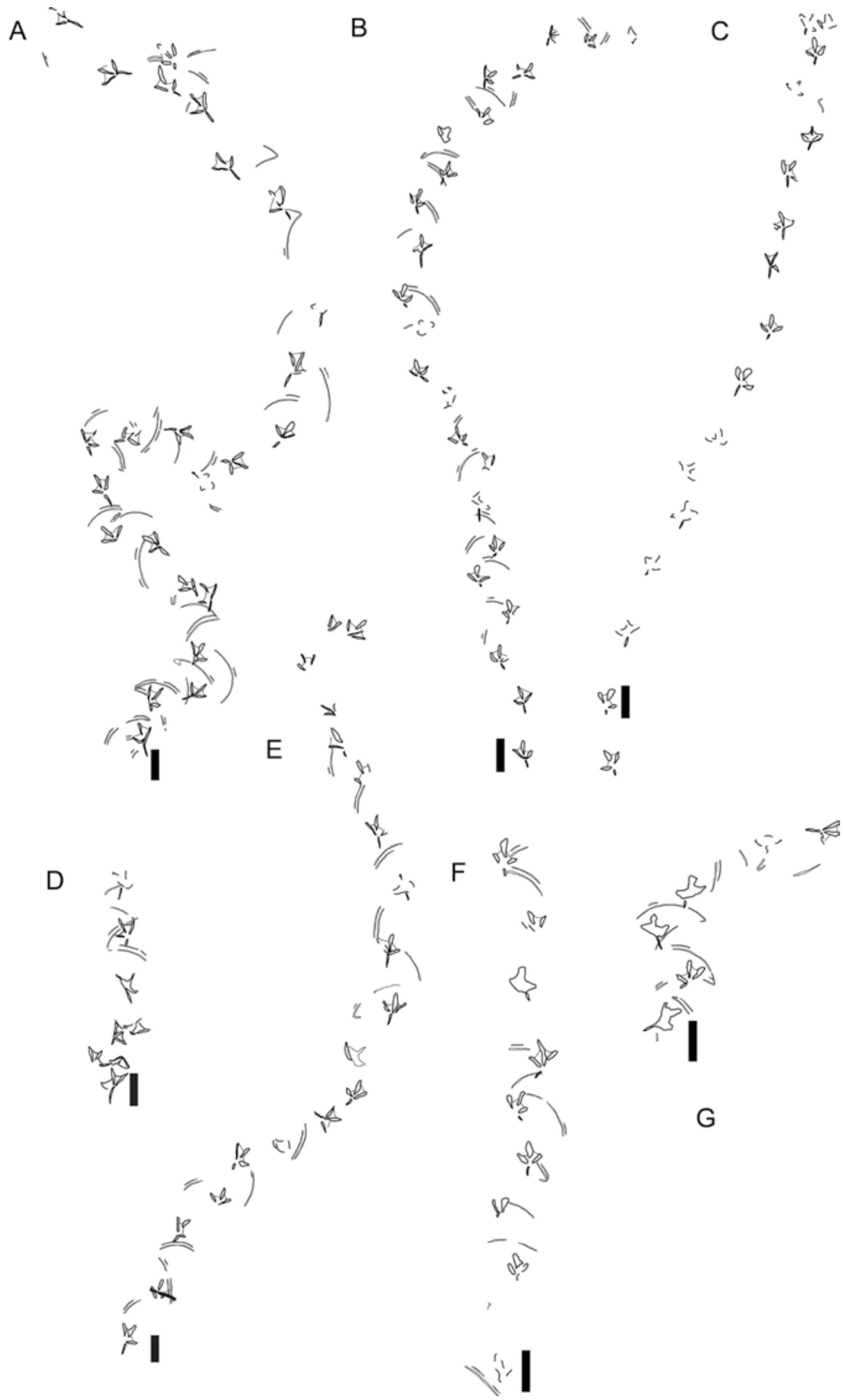

Fig.1 Line drawings of the webbed-footed trackways and associated arcuate bill traces
A. EH1 trackway 1; B. EH1 trackway 2; C. EH1 trackway 3; D. EH1 trackway 4; E. EH1 trackway 5; F. EH1 trackway 6; G. Specimens no. IB41-1; A-F are from Exhibit Hall 1 (EH1), G is from a storage room in the lower level of the building (IB41-1); scale bars = 8 cm

2012). Lim et al. (2000) was the first international publication to discuss the GISE tracksite, and mentioned feeding traces. The majority of tracks studied are housed at GISE; however, a small sample (KS064, NHC-IC-002a, NHC-IC-003a, NHC-IC-004) is currently housed at the Natural Heritage Center in Daejeon, Republic of Korea.

GISE tracks are assigned to *Koreanaornis hamanensis*, *Koreanaornis* sp., and *Ignotornis gajinensis*. Tracks belonging to *Goseongornipes* and several unnamed morphotypes are also present. Specimens used in this study are in the Exhibit Hall 1 (EH1) floor, which includes 6 trackways (Fig. 1); Exhibit Hall 2 (EH2), which includes 3 trackways (Fig. 2), KS049, GS021, GS012, GS018, GS007, IB41-1, KS064, NHC-IC-002a, NHC-IC-003a, and KS019 (Fig. 3). The EH1, KS049, GS012, GS021, GS018, GS007, and IB41-1 specimens are assigned to *Ignotornis gajinensis* (Kim et al., 2012). KS064 is assigned to *Koreanaornis* sp. (Falk et al., 2010).

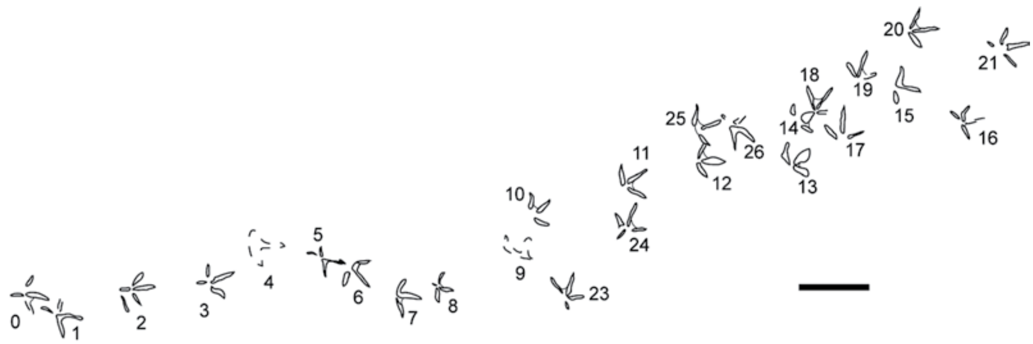

Fig. 2 Numbered line drawing showing *Goseongornipes* tracks on the slab of EH2
Tracks 0–16, 26 represent trackway 1, 17–22 (track 22 not shown) trackway 2, and 23–25 trackway 3
Scale bar = 8 cm

All specimens had single-track and multitrack measurements performed: 1) angle of divarication between toes II and III, III and IV, and II and IV; 2) length of toes II, III, and IV; 3) width of toes II, III, and IV; 4) foot length; 5) foot width; 6) pace length; 7) stride length; 8) pace width; 9) angle of divarication from the midline (Fig. 4). These measurements were used to classify the track and to identify behaviors.

A total of 294 footprints were measured; 118 assigned to *Ignotornis* and are referred to as spoonbill-like traces (S.I. table 1), 132 assigned to *Koreanaornis* (S.I. table 2), 31 assigned to *Goseongornipes* (S.I. table 3), and 13 are unassigned due to the small sample size (S.I. table 4). Several trace fossils associated with these tracks were also measured and are represented in tables alongside the tracks with which they are associated.

3 Results

3.1 Spoonbill-like traces

Sixty-three often-paired arcuate traces are associated with 118 incumbent anisodactyl,

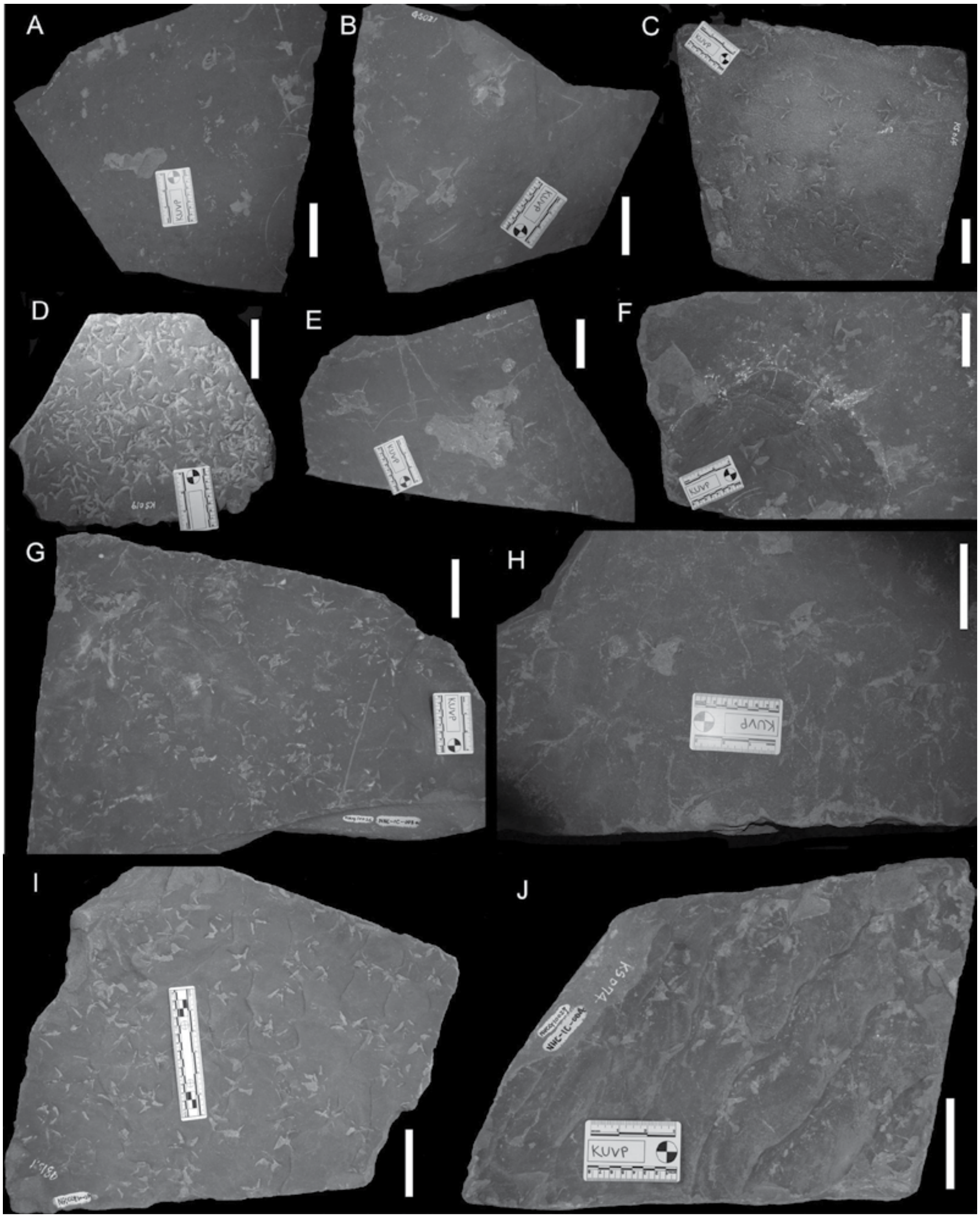

Fig. 3 Plate of isolated specimens
A. GS007; B. GS021; C. KS064; D. KS019; E. GS012; F. KS049; G. NHC-IC-003a; H. GS018; I. NHC-IC-002a (KS0180); J. NHC-IC-004 (KS074); scale bars = 8 cm

webbed-footed (palmate) tracks (S.I. table 1). The footprints had an average foot length (FL) of 43.9 mm, and an average foot width (FW) of 55.55 mm. Table 1 displays the results of all single-track measurements for all specimens. Toes II and IV often exhibit inward curvature typical of webbed-footed birds (S.I. fig. 4).

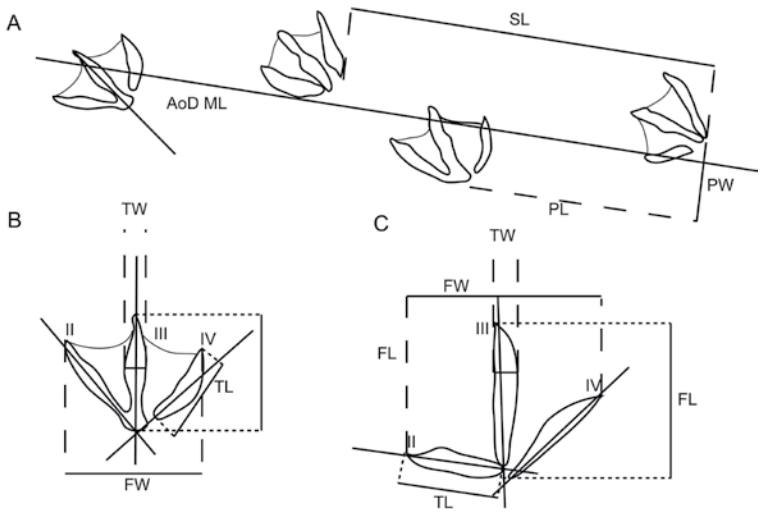

Fig. 4 Line drawings of measurements taken on the tracks
A. multitrack measurements; B. single-track measurements on webbed-footed tracks, note how the AOD measurement is modified for the curvature of the toes; C. single-track measurements on nonwebbed feet
Abbreviations: AoDML. angle of divarication from midline; SL. stride length; PL. pace length; PW. pace width; FW. foot width; FL. foot length; TL. toe length; TW. toe width; II. toe 2; III. toe 3; IV. toe 4

Table 1 Average single track measurements from each specimen used in this study

Specimen	TIIIL (mm)	AOD (°)	FL:FW
EH1	30.9	109.92	0.796
KS006	20	116.3	0.763
NHC-IC-003a	17.5	114.9	0.769
NHC-IC-004	20.3	125.5	0.713
NHC-IC-002a	19.1	125.5	0.711
KS064	24.8	108.8	0.77
EH2	25.2	126.9	0.738
KS005	24	117.7	0.72
GS073	24.97	117.8	0.784
GS068	27.5	133.3	0.787
KS104	28	94.9	0.87

TIIIL. toe III length; AOD. angle of divarication; FL:FW. foot length:foot width ratio.

Multiple track measurements on the six individual EH1 trackways (Fig. 1A–F) and other specimens in this study are summarized in Table 2. Trackway 1 contains 22, trackway 2 is the longest, consisting of 23 footprints, trackway 3 has 16 tracks, trackway 4 is the shortest, with 9 tracks, trackway 5 contains 20 tracks, although only 16 were measured, and trackway 6 contains 11 tracks (see online S.I. for full dataset). Spoonbill-like trackway IB41-1 contains

6 tracks. The Exhibit Hall block specimens (KS049, GS012, GS021, GS018, and GS007, see Fig. 3) were largely isolated tracks and arcuate traces, except for GS018, which contains 6 tracks. The average PL was 123.1 mm, the average PW was 22.9 mm, and the average SL was 250.5 mm.

Table 2 Average multi-track measurements from each specimen used in this study (mm)

Specimen	Trackway #	PL	PW	SL
EH1	1	106	52	221.1
	2	96.7	49.1	199.7
	3	135.5	23.3	271.4
	4	79.1	37	151.1
	5	120	28.8	255.2
	6	101.6	41.8	212.1
IB41-1	1	88.6	68.7	172
NHC-IC-003a	1	63.9	13.2	105
	2	66.5	15.9	113.6
	3	81.1	8	150.8
	4	90.6	26.3	107
	5	41.9	28.2	68
NHC-IC-002a	1	56.8	N/A	106
	2	60	N/A	116.7
KS064	1	35.6	31.4	74.15
	2	31.4	34.4	45.5
	3	34.5	80.2	20.3
	4	80.6	29.8	158.2
EH2	1	66.9	28.8	141.2
	2	63.2	27.9	121.9
	3	114.2	13.8	236

PL. pace length; PW. pace width; SL. stride length.

The average length of the upper arcuate trace for all spoonbill-like specimens was 49.2 mm, and the average width was 2.04 mm. The average length of the lower arcuate trace was 86.9 mm, and the average width was 2.7 mm. The average distance between the upper and lower traces was 6.6 mm.

3.2 *Koreanaornis* and associated traces

Specimens KS006, NHC-IC-002a, NHC-IC-003a and NHC-IC-004 are assigned to *Koreanaornis*. Invertebrate traces are associated with these trackways and, in the case of NHC-

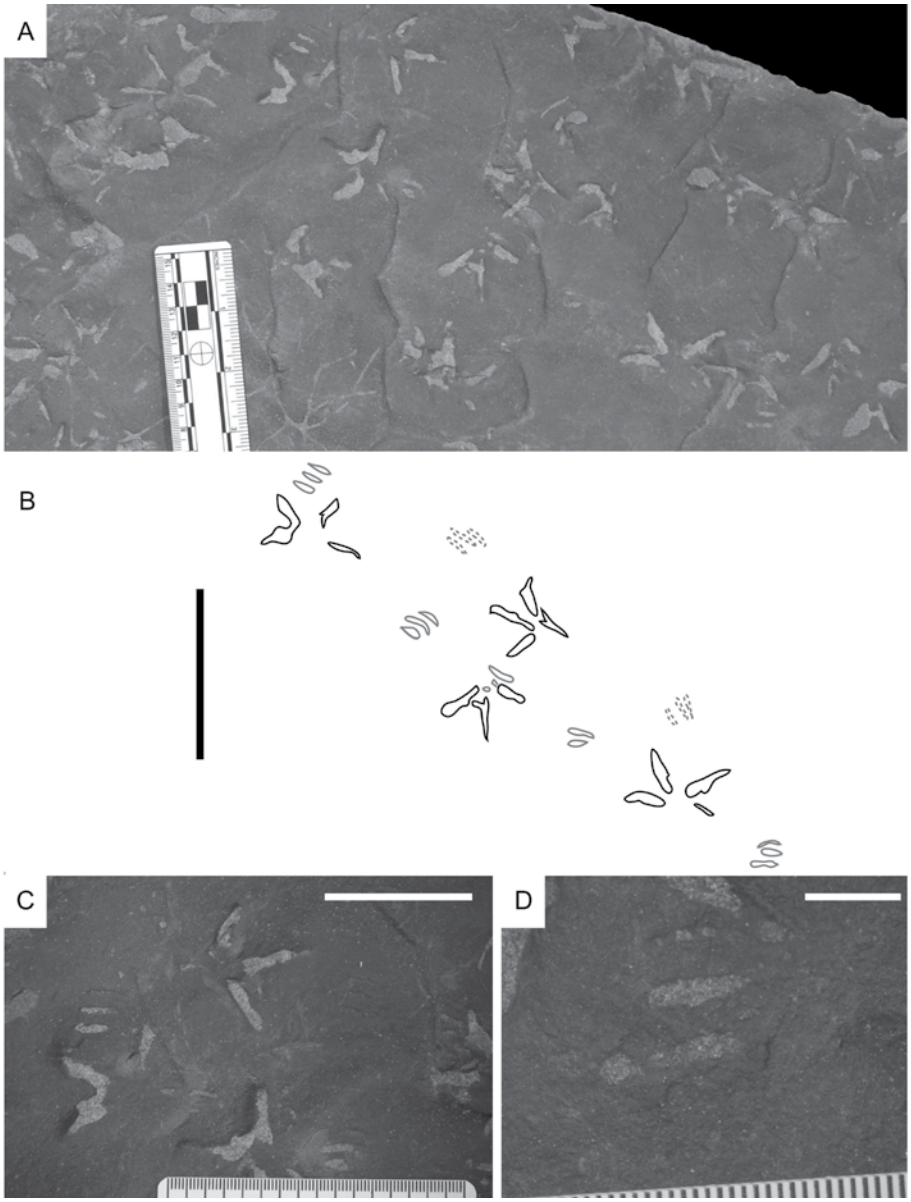

Fig. 5 Parallel enigmatic traces from NHC-IC-002a
A. paired traces associated with a shorebird-like trackway; B. line drawing of A, scale bar = 5 cm; C. closer view of enigmatic traces, scale bar = 4 cm; D. close up of enigmatic traces showing teardrop to elongated oval shaped morphology, scale bar = 8 mm

IC-002a, groups of two-to-three parallel to subparallel enigmatic traces (Fig. 5; S.I. table 5).

KS006 contains many incumbent anisodactyl tracks, however, only 7 measured as a large number of *Koreanaornis* specimens had already been examined (Table 1). NHC-IC-003a contains 60 incumbent anisodactyl tracks, separated into 5 trackways and several isolated tracks (Fig. 6; S.I. table 2). NHC-IC-004 contains 12 incumbent anisodactyl tracks with no

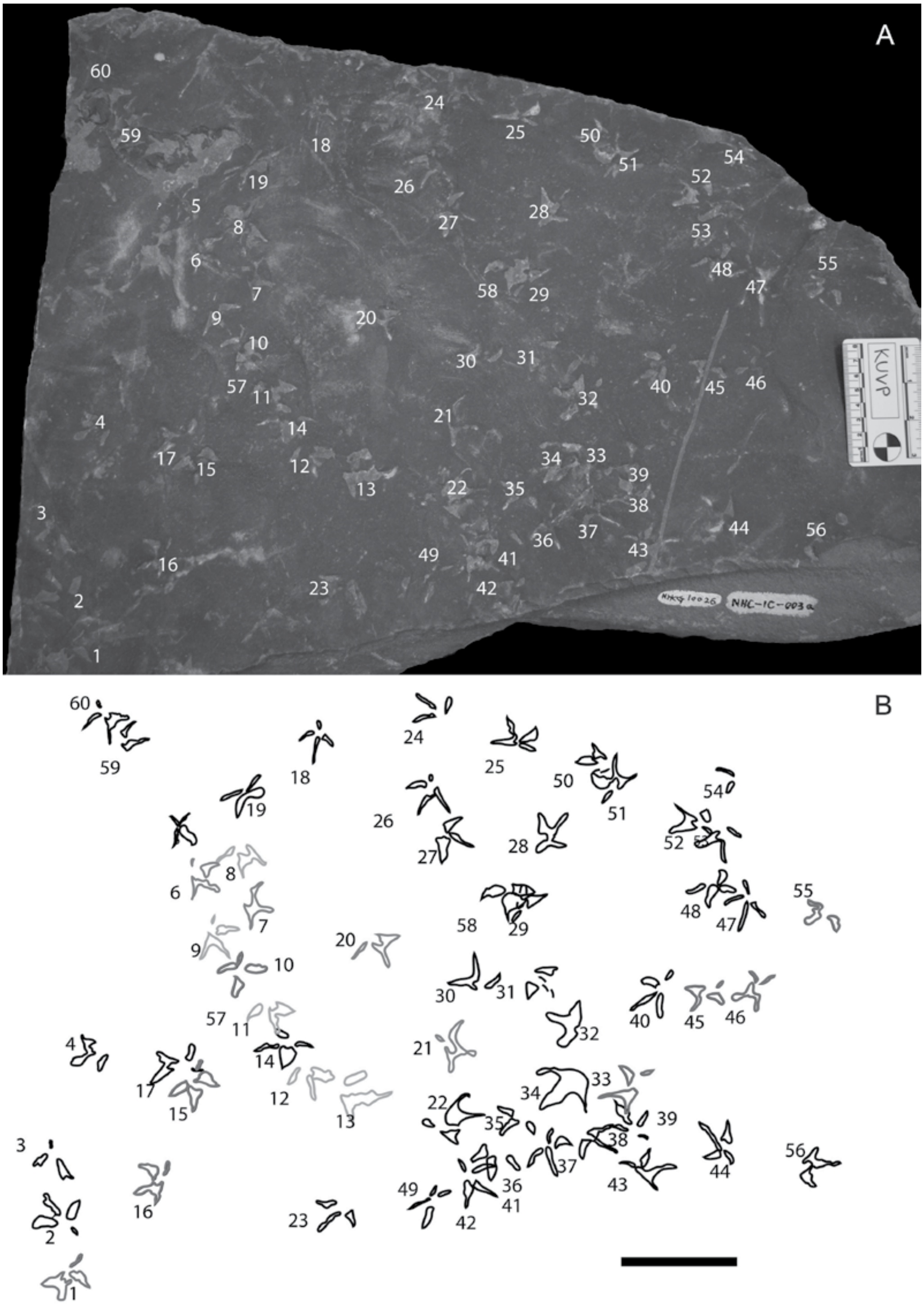

Fig. 6 Photograph (A) and line drawing (B) of NHC-IC-003a

Different shades represent different trackways measured; some tracks belonging to shaded trackways were not included in initial analysis and, therefore, not shaded; scale bar = 8 cm discernable trackways. Distinct ripple marks are present on this specimen. NHC-IC-002a contains 53 individual tracks, two short trackways designated as typical (1) and atypical (2)(Fig. 7; Table 2), and several two-to-three parallel to subparallel linear traces (Fig. 5). The average angle of divarication from the midline (AoDML) of the normal trackway is 15.7°, and the average AoDML of the abnormal trackway is 21°.

The enigmatic traces associated with NHC-IC-002a are either paired or triad. There are a total of six measured clusters (S.I. table 5). These traces are teardrop shaped or elongated ovals and appear to occur alongside a trackway (Fig. 5A). The average length of these enigmatic traces is 8.4 mm, although in some cases slightly oblique curvature makes exact length difficult to measure. The average thickness of these traces at their greatest width is 1.9 mm, and the average distance between these traces is 2.6 mm.

3.3 KS064: *Koreanaornis* sp. and associated traces

The specimen KS064—described as *Koreanaornis* sp. by Falk et al. (2010)—may be attributable to *Goseongornipes* due to the presence of a small amount of webbing between toes III and IV (S.I. fig 5); their size range, however, is well within the *Koreanaornis* range: average FL of 24.8 mm, which is skewed slightly by the presence of one very small track with a FL of 16 mm (see Fig. 8). The average FL:FW is 0.77, which is also within the range of the tracks attributable to *Koreanaornis*. The average AOD is 108.8° (Table 1). Unlike *K. hamanensis*, there is prominent webbing between toes III and IV in *Goseongornipes*, a strong metatarsal pad impression—which can also be found in *Koreanaornis*, but is not described as a defining feature—and a longer hallux. *Koreanaornis* often lacks a hallux. Approximately half of the tracks on KS064 possess such a feature, however, and the average hallux length is 9.07 mm, which is approximately the length of the hallux in *Goseongornipes* based upon the line drawing in Lockley et al. (2006).

These tracks are divided into four trackways (Fig. 8B; Table 2). Trackway one contains 8–10 tracks, although the last two tracks in the trackway questionably belong with the others. Trackway two contains 4 tracks, and trackway 3 contains 6–8 tracks. The affinity of the first two tracks of trackway 3 is difficult to determine, as they are somewhat unusual. Trackway 4 includes 6 tracks.

3.4 *Goseongornipes* (EH2)

Thirty-one incumbent anisodactyl tracks attributed to *Goseongornipes* by Kim et al. (2012) are found on the Exhibit Hall 2 (EH2) slab (Fig. 2). These tracks are divided into 3 trackways (Table 2). Trackway 1 contains 16 tracks, trackway 2 contains 6 tracks, and trackway 3 contains 3 tracks.

3.5 Unassigned tracks

KS005, GS073, GS068, and KS104 are all separate blocks of tracks from EH2 (Fig. 9; S.I. table 4). They are currently unassigned to an ichnogenus due to a relatively small sample size.

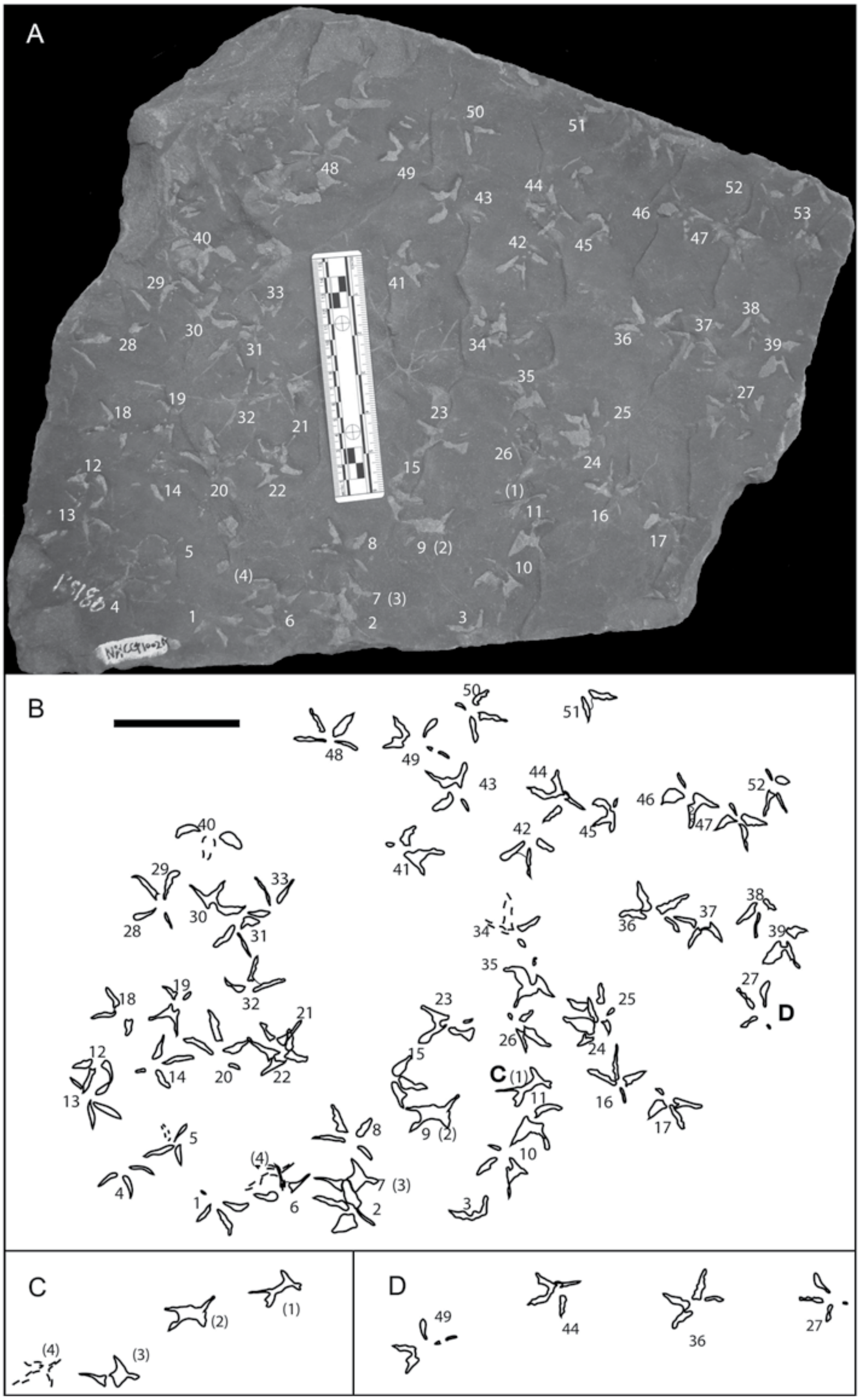

Fig. 7 NHC-IC-002a

A. photograph of specimen; B. line drawing of specimen, scale bar = 8 cm; C. trackway with abnormal morphology; D. representative trackway with normal track morphology

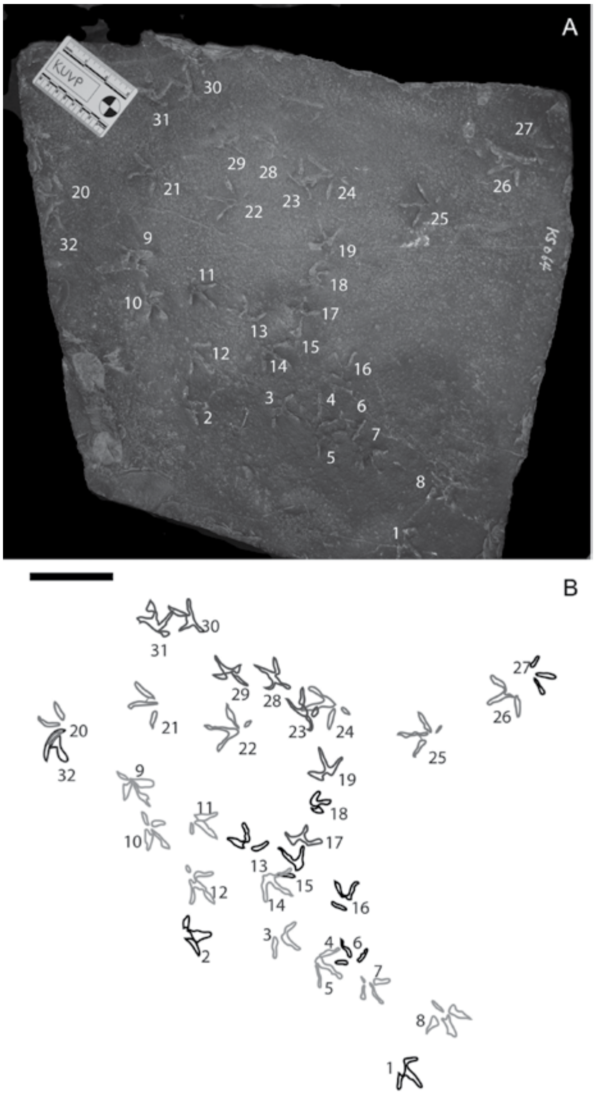

Fig. 8 Photograph (A) and line drawing (B) of the tracks and trackways of KS064
Different trackways are represented as different shades of grey; scale bar = 8 cm

The tracks of KS005 have an average toe III length of 24 mm, an average AOD between toes II and IV of 117.7°, and an average FL:FW of 0.72. There is no webbing present, and many tracks possess a hallux, which has an average length of 8.9 mm.

The tracks of GS073 have an average toe III length of 24.97 mm. The average AOD between toes II and IV is 117.8°, and the average FL:FW is 0.784. All tracks lack a hallux. Some tracks have faint impressions of short semipalmate webbing between toes III and IV.

The tracks of GS068 have an average toe III length of 27.5 mm. The average AOD between toes II and IV is 133.3°, and the average FL:FW is 0.787. Some tracks possess a hallux, which has an average length of 14.8 mm. These tracks lack any impression of webbing.

KS104 possesses a new avian track morphotype with semipalmate webbing. The webbed portion of the toe is less than 1/2 the length of the unwebbed portion. Only one track is available for study, with a toe III length of 28.0 mm, an angle of divarication between toes II and IV of 94.9°, and a FL:FW ratio of 0.87.

4 Discussion

4.1 Types of avian morphologies present

The presence of seven morphotypes—*Koreanaornis*, *Goseon-gornipes*, *Ignotornis*, KS005, GS068, KS104, and GS073—indicates a high avian diversity. *Koreanaornis* and *Goseongornipes* are similar overall, representing smaller, shorebird-like birds similar to sandpipers and plovers. These ichnogenera are present in very large quantities, especially

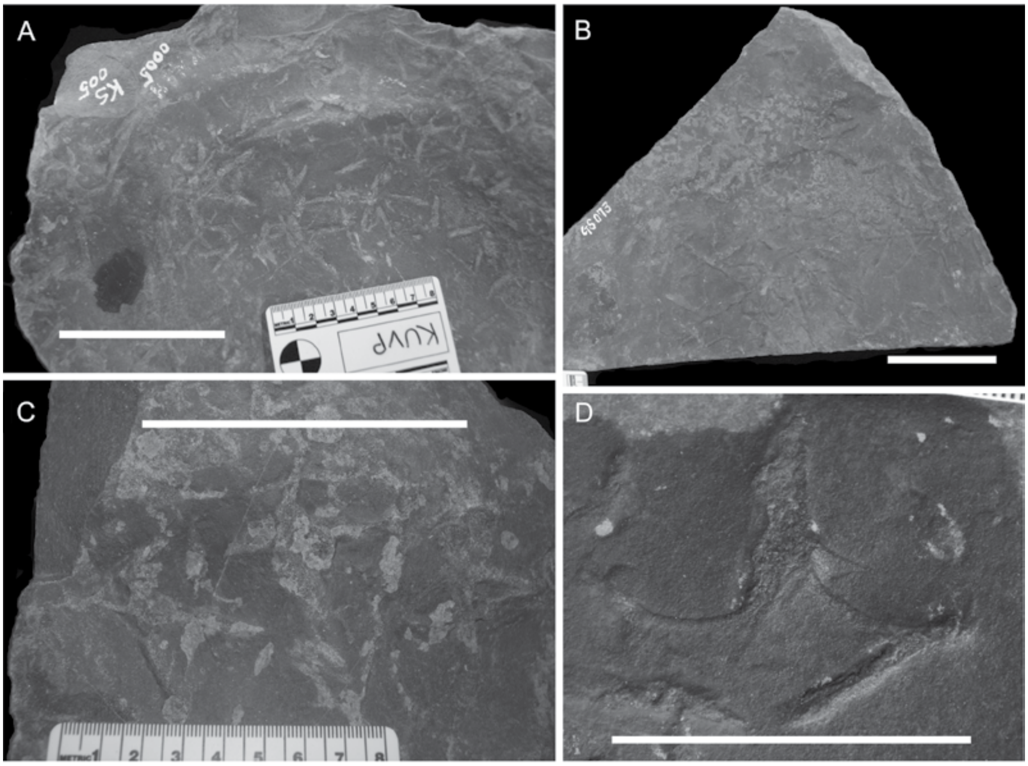

Fig. 9 Photographs of specimens currently unassigned to an ichnogenus
A. KS005, scale bar = 8 cm; B. GS073, scale bar = 8 cm; C. GS068, scale bar = 8 cm; D. KS104, scale bar = 4 cm

Koreanaornis.

Due to the highly distinctive feeding traces, *Ignotornis gajinensis* represents an entirely unknown avian morphotype from the Mesozoic. No bird with a spoonbill-like skull has been reported from the Cretaceous (Lockley and Harris, 2010). There are no known fossil spoonbills, although subfossil remains are known from Australia (Baird, 1990). The evidence at GISE indicates a much earlier evolution of a spoonbill-like ecomorph. Tracks associated with the arcuate traces are strongly webbed, whereas spoonbills have semipalmate feet with webbing that is not extensive (Swennen and Yu, 2004). Tracks that do not have webbing can appear webbed, depending on the sediment consistency (Elbroch and Marks, 2001; Falkingham et al., 2009); semipalmate tracks of modern spoonbills appear alongside arcuate bill traces left by their feeding activities (Swennen and Yu, 2005). The Cretaceous spoonbill-like ecomorph may have possessed webbed feet, as webbing appears in well-preserved specimens (S.I. fig. 6). The feet of the spoonbill-like bird were semipalmate.

Kim et al. (2012) assigned EH2 to *Goseongornipes markjonesi* based on morphology. Some of the EH2 tracks—specifically those that lack a hallux impression and have the semipalmate webbing poorly preserved—superficially resemble *Aquatilavipes*, except that their size is much smaller. Their AOD is smaller than that recorded for the *Goseongornipes* holotype (126.9° vs. 140°–150°). The webbing on the tracks of EH2 is often less distinct than that indicated on the holotype specimens of *Goseongornipes*. These specimens may belong to a new ichnospecies of *Goseongornipes* based on the characters present.

KS005 is similar to *Koreanaornis* except that it is larger—toe III is 24 mm long instead of the average 20 mm long—and there is a more pronounced and caudally directed hallux present (S.I. fig. 7). Tracks of KS005 lack the distinctive semipalmate webbing that defines *Goseongornipes*. These tracks represent another type of shorebirdlike bird at GISE.

The tracks of GS068 are similar to *Koreanaornis*, but possess a longer hallux—*Koreanaornis* often lacks a hallux—and are larger, with an average toe III length of 27.5 mm as compared to 20 mm in *Koreanaornis*. These tracks may represent a different ichnospecies of *Koreanaornis*. These tracks represent a fourth type of sandpiper- or plover-like bird at GISE.

The tracks of GS073 are approximately the same size as those found on KS005, but are morphologically different. All tracks lack a hallux; where the tracks of KS005 lack a metatarsal pad impression and possess a small hallux, the tracks of GS073 all possess a clear metatarsal pad impression, and many have claw impressions preserved. There are also faint traces of semipalmate webbing present on some of the tracks, which is not as common or readily pronounced in *Koreanaornis*. These tracks represent a type of shorebird more similar to a plover or other medium-sized shorebird with an elevated or absent hallux. These tracks are unlikely to be referred to *Aquatilavipes* based only on the presence of semipalmate webbing.

KS104 represents a morphotype that is nearly identical to modern avocets (e.g., *Recurvirostra americana*, Elbroch and Marks, 2001). This morphotype lacks a hallux entirely but possesses a very clear metatarsal pad impression, and toes II, III, and IV are bound by webbing, although the webbing is not as extensive as seen on *Ignotornis gajinensis*. The lack of a hallux combined with the non-extensive semipalmate webbing between three toes is different in comparison to all other morphotypes described from GISE.

4.2 Types of behaviors interpreted from the trackways

There are a number of behavioral interpretations possible based on feeding traces not previously described from GISE, and non-feeding behaviors are also present that can be interpreted based on comparison to modern avian behaviors. The non-feeding behaviors are interpreted empirically, as there are limited sources on modern avian tracks, and no quantitative study accurately measures the traces of modern birds and links them to the behavior produced. The most numerous and important feeding trace is the arcuate traces interpreted as scything behavior alongside the tracks of *Ignotornis gajinensis* (Lockley and Harris, 2010). These Cretaceous trackways are very similar in morphology, proportion, and stride length to those of modern black-faced spoonbills (*Palatea minor*) studied by Swennen and Yu (2005: fig. 2a); however, they are smaller than those belonging to *P. minor* (toe III length of 26–43 mm vs 60–70 mm for *I. gajinensis* and *P. minor*, respectively). The *Ignotornis* trackways in our study have an average SL of 216.6 mm and a standard deviation of 41.8, whereas modern *P. minor* trackways have an average SL of 263 mm with a standard deviation of 32 (Swennen and Yu, 2005). Scything behavior is an important behavioral addition to the track record of Cretaceous birds, indicating that the range of avian-foraging behaviors (i.e., probing, pecking, foot shuffling; Lockley et al., 2009; Falk et al., 2010) in water-margin environments is potentially more extensive than previously thought.

Among the arcuate traces of EH1 Trackway 1 is a small, elliptical indentation between tracks 7 and 8 (Fig. 10). Spoonbills have been reported to make sharp, jabbing motions when prey is detected beyond the tip of the bill (Swennen and Yu, 2005:23). The elliptical indentation may be a peck or jabbing form of prey-capture movement, given the broad, flattened beak morphology of the spoonbill and a comparison of the indentation with the frontal view of the spoonbill beak (Swennen and Yu, 2004: fig 1d). This is evidence that the *Ignotornis gajinensis* tracemaker did possess a distally flattened, broad bill. No trace fossil of this jabbing method has been reported previously. The presence of this jabbing behavior indicates that the feeding methodologies of spoonbill-like birds were likely identical to modern spoonbills, and that they used both a scything and a jabbing method of prey capture.

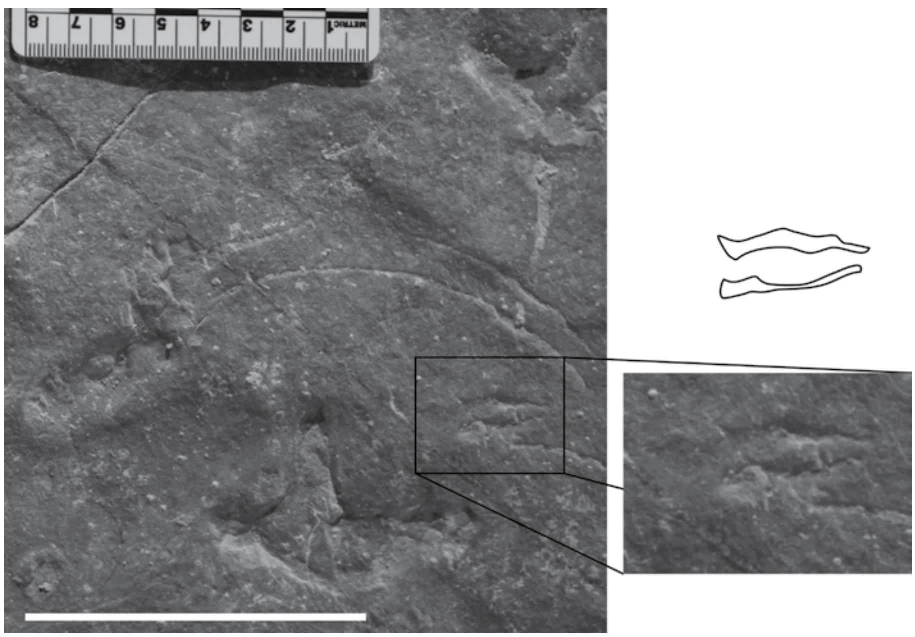

Fig. 10 Elliptical beak impression next to EH1 trackway 1 (scale bar = 8 cm)

Another behavior reflected in the spoonbill-like traces can be seen in EH1 trackway 4, which consists of 9 tracks (Fig. 1D). This trackway has an abrupt beginning interpreted as a landing. The first three tracks suggest that the bird landed and made a stutter step (third track, which is a partial track) before beginning to forage. The third track may represent the bird producing a trace with a partially clenched foot, based on the length of the digit impressions.

The foraging behavior is represented by the paired arcuate traces recorded later in the trackway.

Trackway 5 of EH1 (Fig. 1E) indicates that the large sauropod tracks found alongside trackway 5 were produced prior to the bird trackways. High concentrations of *Koreanaornis* and other bird tracks found within the sauropod tracks support this interpretation (Fig. 11). Trackway 5 contains a series of tracks exhibiting the spoonbill-like scything behavior. The bird then steps down into the sauropod track (Fig. 11C). No arcuate traces are associated with the trackway in the sauropod track; the lack of feeding traces may reflect relatively deeper water in the sauropod track. This interpretation is supported by the observations of modern spoonbill feeding behaviors, which are only recorded as arcuate traces in very shallow water (Swennen and Yu, 2005).

The association of avian tracks, trackways, and feeding traces with sauropod tracks and trackways may suggest that birds were trailing megaherbivores. This type of trailing behavior is seen in birds today in Africa that follow large herbivores (Dean and MacDonald, 1981), on the ocean following feeding cetaceans (Evans, 1982) and the boat wakes (Hudson and Furness, 1989; Tasker et al., 2000), and where plowing disturbs the soil (Welham and Ydenberg, 1988; Tasker et al., 2000). Trace-fossil associations in the Haman Formation are interpreted as follows: as sauropods moved through the water, they stirred up the sediment and benthic invertebrates that were foraged upon by the birds that followed in the wake, snapping up the disturbed prey. Similar associations were first reported by Lockley et al. (1997).

The tracks of EH2 show mostly straight-line to slightly meandering walking. One long trackway is intersected by two other shorter trackways and, therefore, behavioral interpretations of the other two trackways are difficult to determine (see Fig. 2). The EH2 tracemaker exhibited typical heron-like foraging behaviors based on variations in PL and SL (S.I. table 6). Herons and other wading birds rarely take regular steps when feeding, and often stop and stand before starting again. Although no traces are present on the EH2 slab to suggest stopping and standing behavior, the intersection of multiple trackways of the same type of tracemaker (if not the same tracemaker) makes such an interpretation more difficult than if all three trackways were isolated.

There are a few interesting behaviors noted on the EH2 slab (Fig. 2). Track 2, originally thought to have a long hallux, is actually a double step; the left foot came down then came back up and was placed a few centimeters forward of its previous position, causing an overlapped track. Toe IV of this first step did not register, and the two toe IIIs appear almost continuous. Only toe II indicates that it is a double step. This bird was likely foraging and, therefore, being careful where it placed its feet. Track 9 has toes that are much thicker than other tracks from this floor slab (Fig. 2; S.I. table 3), and between the toes there are small raised areas of sediment (S.I. fig. 8). The particularly long pace length between tracks 8 and 9 (89.5 mm) and tracks 10 and 11 (103.2 mm, see online sup. info.), and the twisted morphology of track 9 may be analogous to a specific type of feeding behavior commonly seen in the reddish egret (*Egretta*

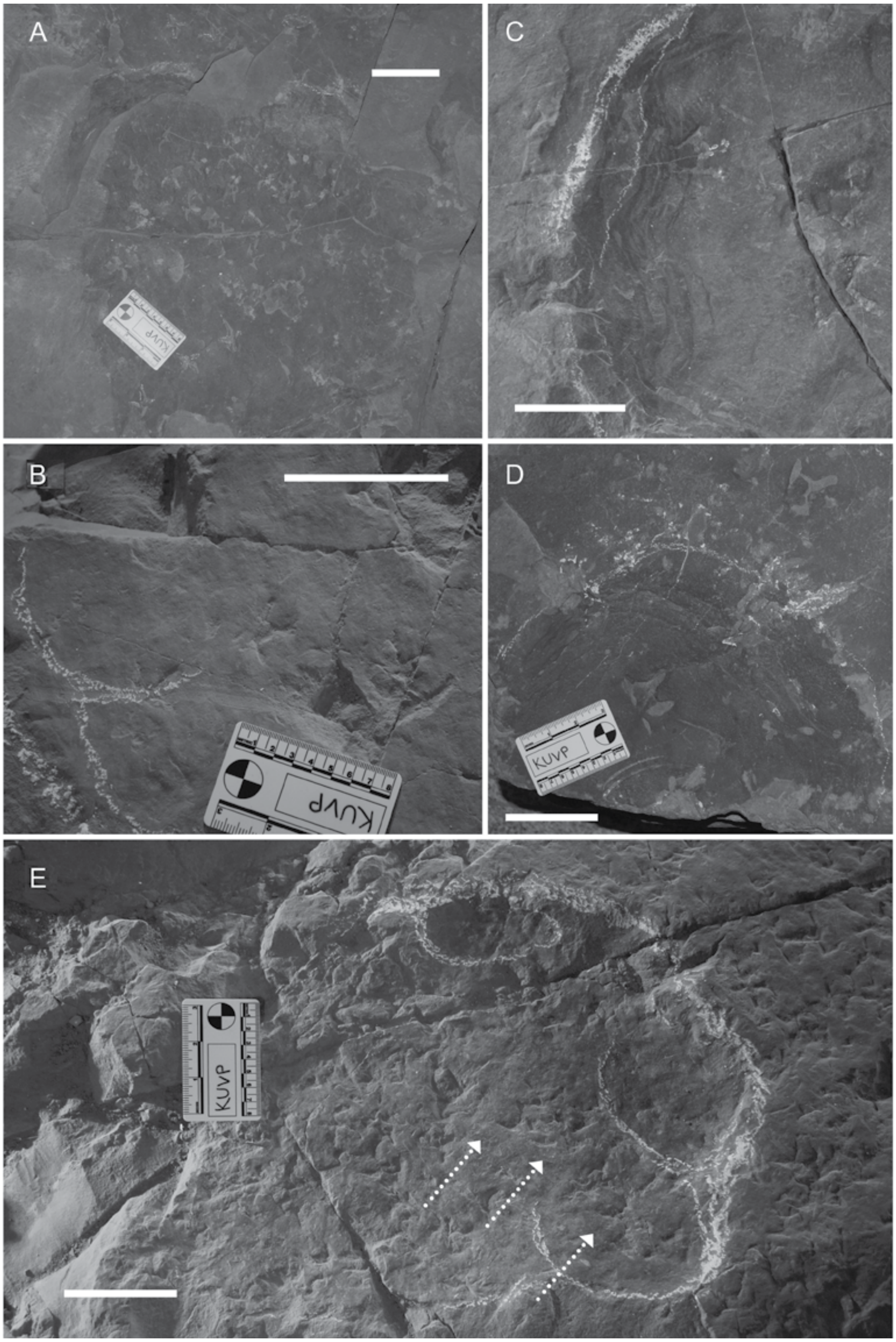

Fig. 11 Bird tracks inside sauropod tracks on EH1
A-B. shorebird-like tracks inside sauropod tracks; C-D. *Ignotornis gajinensis* tracks found inside sauropod tracks, note that in C the bird is stepping down into the track, whereas in D the bird is stepping up out of it; E. sauropod track with many shorebird-like tracks (arrows); scale bars = 8 cm

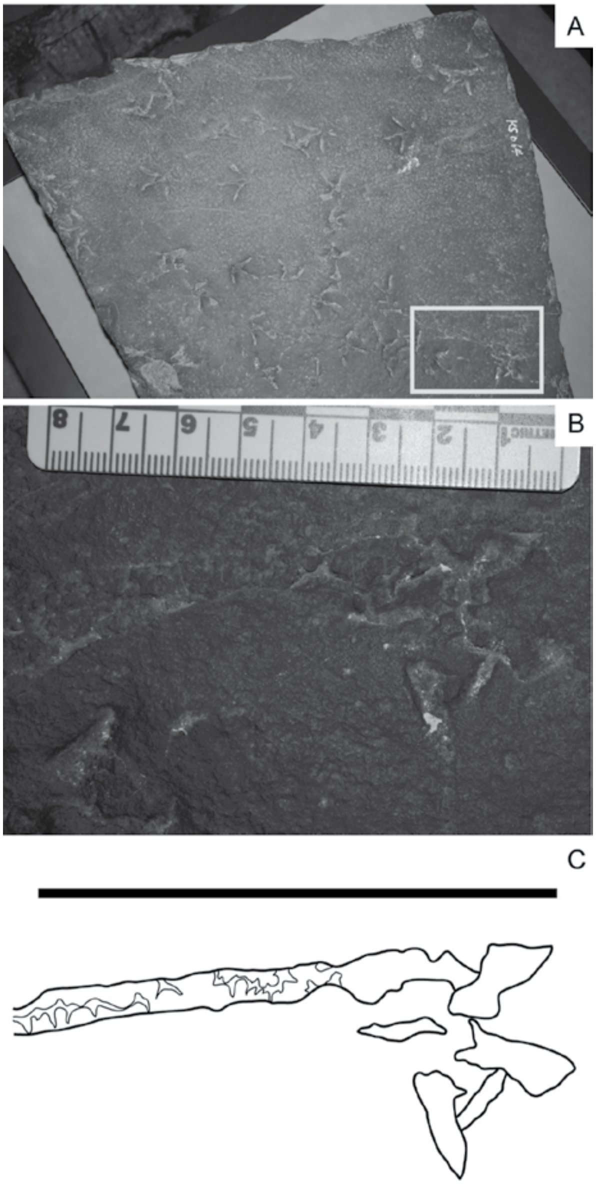

Fig. 12 Intersection of an invertebrate trace (cf. *Steinichnus*) and a bird track
A. KS064, with area of B boxed in; B. intersection of cf. *Steinichnus* and bird track, scale in cm; C. line drawing of B, scale bar = 8 cm

rufescens) of North America. This heron will leap, hover, and rake its feet—stirring up sediment to either frighten or confuse prey species—before landing to capture prey species (Meyerriecks, 1959; Kushlan, 1976).

Falk et al. (2010) provided a preliminary description of the behaviors of KS064. The peel described in that study, however, was partial, and did not allow for a complete interpretation of the behaviors of the tracemakers. Several behaviors ranging from simple running to feeding traces are present on the slab (Fig. 8) from which the partial peel was made. The trackway that has tracks labeled as having an atypical morphology (tracks 9 and 10) may represent a landing trace (Fig. 8). They are ~ 8 cm from the broken edge of the slab, however, no other tracks posterior to them appear to be associated with this trackway. They have relatively narrow angles of divarication—88° and 96°, respectively—and have long halluxes (12 and 13.5 mm, respectively). The next track in this series, track 11, lacks a hallux but appears to be impressed deeper into the sediment than the other tracks (Fig. 8), and tracks 10–11 have an extremely short PL and narrow PW (S.I. table 7). Track 11 could show the animal slowing quickly as it took the next step after landing. Track 12, the next track in this sequence, is entirely typical, indicating the landing process was complete and the bird was walking normally.

At the end of the landing trackway, track 8 intersects with an invertebrate trace (cf. *Steinichnus*; Fig. 12). Toe III of track 8 has a greater width than that of any other track except for track 31 (S.I. table 2). The track itself seems smeared, as if the animal pivoted in place

(Fig. 12, see also Fig. 8). After this point, the invertebrate trace is not present. There is an elliptical impression on the surface between toes III and IV that is not webbing, and appears morphologically similar to the peck marks previously reported from the Haman Formation (Falk et al., 2010). This association of traces and tracks suggests that the bird was hunting the invertebrate, and perhaps captured it.

KS019 tracks were not measured due to extreme track density (Fig. 13), however, KS019 does show an important behavior. Probe marks have been reported from the Haman Formation and from Upper Cretaceous deposits from northern North America (Falk et al., 2010; Fiorillo et al., 2011). The probe marks previously reported from the Haman Formation, however, were isolated, indicative of a different pattern of feeding than the type seen from the Upper Cretaceous Cantwell Formation, which show the probe marks in more of a cluster or a group (Fiorillo et al., 2011: fig. 13). Elbroch and Marks (2001) illustrate several kinds of probing: isolated, clustered, and linear probing. Isolated and clustered probes are usually performed while the bird has paused; linear probing is a continuous action while the bird walks. KS019 shows several areas of probe clusters (Fig. 13B–C), a phenomenon previously unreported from Lower Cretaceous rocks.

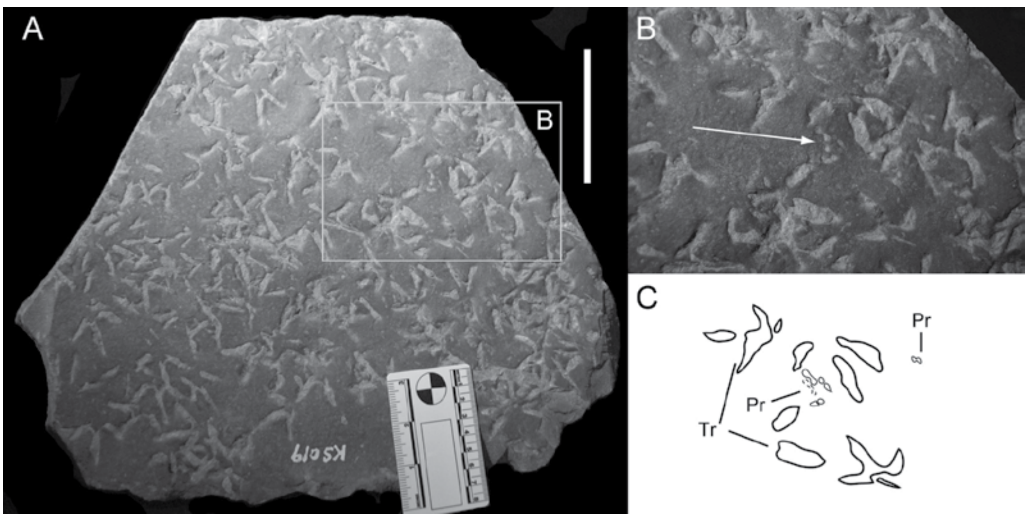

Fig. 13 KS019

A. photograph of the specimen, the box indicates area defined in B; B. close up of a probe cluster (arrow); C. line drawing from B; Tr. track; Pr. probe; scale bar = 8 cm

Other specimens of *Koreanaornis* sp. (NHC-IC-003a, NHC-IC-002a) show a variety of behaviors. The series of paired to triplet parallel to subparallel traces on NHC-IC-002a (Fig. 7) may represent 1) drag marks of feathers, either primary feathers or tail feathers or 2) swimming traces of a reptilian trackmaker the size of a small lizard. The bird that produced feather marks might have been injured, although there is no evidence in the trackway of a limp or other injury. Another explanation is the broken-wing-defense commonly seen in plovers. The male or female will feign a broken wing in order to draw a predator away from the vulnerable offspring. Reptile swim traces are often preserved as 3–5 thin, decurved lines following a central track midline (Hunt et al., 1990; Melchor and Sarjeant, 2004; Milner et al., 2006).

NHC-IC-002a also contains tracks that represent atypical shorebird track morphology (Fig. 7C). The exact behavioral cause of this morphology is unknown, as this morphology has not yet been observed in modern bird tracks. These types of tracks may represent a landing trackway, or a very fast running trackway, based on a similar morphology seen on KS064. The trackway seen on NHC-IC-002a is only four tracks long and terminates due to the broken edge of the slab. This atypical trackway morphology is unlikely to be due to the presence of a different type of bird, based on comparisons to trackways from KS064.

NHC-IC-003a contains an oval-shaped, slightly depressed area, bounded on one side by a crescent-shaped indentation and on the other by what appears to be a small linear trough (S.I. fig. 9). Interpretation of these features is difficult without multiple examples.

4.3 Implications for avian evolution based on behavioral evidence

Behavioral evidence from GISE indicates a high diversity of birds (Table 3). Ornithurine birds likely produced these tracks, as they are the dominant water birds of the Early Cretaceous (Zhou and Zhang, 2007). The presence of scything traces and peck and probe marks also indicate that several modern feeding behaviors had evolved by the Early Cretaceous. The 7 morphologies in the Haman Formation at GISE support these interpretations.

Table 3 Examples of rock units with low diversity, high diversity, and very high diversity of fossil birds

Formation	Location	Age	Diversity	Ichnogenera
Dakota	Colorado, USA	Late Cretaceous	High	*Ignotornis* *Koreanaornis* *Aquatilavipes*
Lakota	South Dakota, USA	Early Cretaceous	Low	*Aquatilavipes*
Gething	British Colombia, Canada	Early Cretaceous	Low	*Aquatilavipes*
Haman	Republic of Korea	Early Cretaceous	Very high	*Koreanaornis* *Goseongornipes* *Ignotornis*, more
Jindong	Republic of Korea	Late Cretaceous	Low	*Jindongornipes* *Koreanaornis*
Uhangri	Republic of Korea	Late Cretaceous	Low	*Uhangrichnus*
Itsuki	Japan	Early Cretaceous	Low	*Aquatilavipes*
Jingchuan	China	Early Cretaceous	Low	*Tatarornipes*
Tugulu (Group)	China	Early Cretaceous	Very high	*Koreanaornis* *Aquatilavipes* *Moguiornipes*, more
Jinhua	China	Late Cretaceous	Low	*Dongyangornipes* *Koreanaornis*

Evidence from GISE suggests that ornithurine birds had a radiation that may have rivaled the enantiornithine birds for its diversity during the Early Cretaceous. Enantiornithines were the dominant birds during the Cretaceous (Zhang et al., 2004) and filled the niches of terrestrial birds. The ornithurine birds were much smaller in diversity according to the body fossil record (Zhou and Wang, 2010); however, they dominate the avian trace-fossil record. There are no known tracks of enantiornithines preserved. This lack of enantiornithine tracks may be an artifact of the lifestyle of these birds, as they were mainly arboreal (i.e., tree dwelling).

Recent studies of avian molecular clocks suggest that the origin of modern bird families took place during the Cretaceous (Pereira et al., 2007; Brown et al., 2008; Pacheco et al., 2011). Some Late Cretaceous fossil birds have been assigned to modern or Cenozoic orders and/or even Cenozoic families (Chiappe and Dyke, 2002; Kurochkin et al., 2002), but no Early Cretaceous birds are thought to belong to extant families or genera. The likelihood of the spoonbill-like tracemaker belonging to the Threskiornithidae is very small, and these tracks are probably the traces of a spoonbill ecomorph—a shallow-water-feeding bird with a spoon-shaped bill.

The majority of Mesozoic avian tracksites are monospecific with relatively few tracks (e.g., Lockley et al., 2001, 2009; Anfinson et al., 2009); however, an increasing number of multi-ichnotaxa sites with high track density are being identified in East Asia (Xing et al., 2011; Lockley et al., 2012; Kim et al., 2012). This may be evidence that East Asia was the center of early avian evolution as suggested by Zhou et al. (2003).

5 Conclusions

The fossil bird tracks of the Lower Cretaceous Haman Formation at GISE show at least seven morphotypes. Associated with these tracks are a variety of feeding behaviors, from isolated probe marks and clustered probing, to pecking, and complex arcuate traces associated with web-footed tracks that are identical to similar traces produced by modern black-faced spoonbills. Other behaviors include landing traces, walking and foraging, and traces of predator-prey interaction. The environment of this locality is interpreted as extremely shallow water (~5–6 cm deep; see suppl. info.) based on comparison of the Cretaceous traces to similar modern avian traces and their environment. The webbed-footed bird tracks and traces were produced under water based on the presence of the arcuate traces, the conditions under which these traces are produced by modern spoonbills, and the lack of mud cracks indicative of subaerial exposure. The incredible morphologic and behavioral diversity of GISE and at other localities from the Lower Cretaceous Haman Formation suggests that the Mesozoic ornithurine radiation was, perhaps, as diverse as the enantiornithine radiation. Ornithurines, however, are preserved in water-margin environments, whereas the enantiornithines dominated terrestrial niches (based on their morphology). Many of the bird tracks at GISE are yet undescribed, in part, due to the sheer amount of material that still needs to be examined. Also, GISE is only one of many bird tracksites in the Cretaceous of the Republic of Korea and other outcrops still need examination.

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韩国哈曼组鸟类足迹化石行为分析及与现代鸟类生态系统的对比

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摘要：韩国下白垩统哈曼组地层中已发现有数个化石点，含丰富的恐龙、鸟类以及翼龙足迹化石，其中一个足迹化石地点位于韩国晋州市的庆尚南道科学教育研究所。1000多个鸟类足迹发现于同一岩层，同时另有数千件零散的标本在博物馆展出或藏于库存中。这些足迹标本显示了生物体在形态学与行为学等方面很高的多样性。本文描述了至少7种不同的形态类型，指示了取食行为(包括啄食、探食、捕食者与被捕食者之间的行为关系), 以及镰刀状痕迹所反映出的着陆与奔跑的不同行为方式。保存的弓状痕迹及伴生的具蹼足迹与现生鸟类黑脸琵鹭(*Palatea minor*)在取食时留下的镰刀状痕迹相一致。单独的啄食及探食痕迹已有相关报道，集群探食痕迹亦有所发现。这个化石地点所保存的鸟类足迹在形态学和行为学上都非常进步，指示了今鸟类与现代鸟类相似的解剖学特征和行为模式。此前根据鸟类骨骼化石的记录，研究者认为反鸟类为早白垩世鸟类的主要类群，然而足迹形态的的高度多样性反映了早白垩世今鸟类已经具有很高的多样性。

关键词：鸟类，行为，探食迹，白垩纪鸟类足迹，鸟化石

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